

## Habitat Use by Sympatric Jaguars and Pumas Across a Gradient of Human Disturbance in Belize

Rebecca J. Foster<sup>1,2,3</sup>, Bart J. Harmsen<sup>1,2</sup>, and C. Patrick Doncaster<sup>1</sup>

<sup>1</sup> School of Biological Sciences, University of Southampton, Southampton, SO16 7PX, UK

<sup>2</sup> Panthera, 8 West 40th Street, 18th Floor, New York, New York 10018, U.S.A.

### ABSTRACT

Jaguars (*Panthera onca*) and pumas (*Puma concolor*) are sympatric across the entire jaguar range, where they coexist in increasingly fragmented landscapes under threat of persecution mainly in response to livestock predation. Pumas are known to inhabit a greater variety of natural habitats than jaguars, but little is known about the influence of anthropogenic factors on the coexistence of these two similar-sized cats. This study compares habitat use of jaguars and pumas in Belize, Central America, using 1380 jaguar and puma photo captures from 3 yr of camera trapping, comprising 64–74 individual jaguars and an unknown number of pumas. Jaguars and pumas did not differ in their use of a large block of relatively homogenous secondary rain forest. However, pumas were scarce outside this forest block, whereas jaguars were detected throughout the human-influenced landscape. Reasons for this discrepancy may include differential tolerance to human disturbance, and resource limitation for pumas outside the forest block. Intra-specific variation in jaguar activity in the form of sex-dependent habitat use was detected across the landscape. Male jaguars were detected at more locations than female jaguars and more frequently at each location, with a declining difference from a 50-fold greater detection in the protected forest, through forest buffer, savannah, pastures, to negligible difference in the disturbed forest.

*Key words:* activity; camera trap; carnivore; coexistence; felid; *Panthera onca*; *Puma concolor*.

UNDERSTANDING HOW LARGE CARNIVORES USE THE HUMAN-MATRIX relative to the remaining contiguous natural habitat is essential for predicting their long-term survival across increasingly human-dominated landscapes. Where multiple carnivores live sympatrically, comparisons of man-modified to natural habitat are valuable for predicting human impact on coexistence. For example, the vulnerability of competitively inferior species within carnivore guilds may increase under pressure from human activity (Creel 2001, Woodroffe 2001). This study focuses on the jaguar (*Panthera onca* L. 1758) and the puma (*Puma concolor* L. 1771), two cats of similar size which coexist throughout the neotropics, a region where current human population growth is second only to Africa (World Resources Institute 2007). Both species attack livestock with resulting persecution by people. Little information exists on the extent to which jaguars and pumas may favor human-influenced landscapes over wilderness, or how anthropogenic factors may influence the coexistence of these two species. This study compares habitat use between the species across an undisturbed protected lowland rain forest and adjacent human-influenced landscape, in Belize, Central America.

Jaguars occupy a variety of habitats including rain forest, pine-oak forest, wet grasslands, mangroves and arid scrub, although they tend to associate with water (Emmons & Feer 1990, Kitchener 1991, Nowell & Jackson, 1996, Reid, 1997, Monroy-Vilchis *et al.* 2009). Although recorded at up to 3800 m asl, they commonly occupy lower-lying land  $\leq$  1200 m (Sunquist & Sunquist 2002). Pumas are found in a wider range of natural environments, covering every major habitat type of the Americas at altitudes up to 5800 m (Emmons & Feer 1990, Nowell & Jackson 1996, Sunquist

& Sunquist 2002). At the biogeographic scale, and discounting human factors, pumas may be considered to have more flexible habits than jaguars. Pumas are well studied in North America (see Sunquist & Sunquist 2002), but relatively under studied in the neotropics (Laundré & Hernández 2009). The few studies of habitat use by pumas and jaguars in sympatry are limited to small sample sizes associated with telemetry, ranging from 3 to 11 cats (Schaller & Crawshaw 1980, Emmons 1987, Núñez *et al.* 2002, Scognamiglio *et al.* 2003). Recently camera-trap data have been used to compare habitat use by these two cats. Harmsen *et al.* (2010) studied trail use of jaguars and pumas in the relatively homogenous environment of a protected Neotropical secondary forest; Monroy-Vilchis *et al.* (2009) supplemented limited camera data with interview data to compare habitat use across a heterogeneous temperate landscape. Here, we present habitat analyses of a uniquely large dataset of > 60 jaguars and multiple pumas, using 977 and 403 independent photo captures, respectively. We used camera traps to monitor activity of both species simultaneously within an undisturbed forest and across a range of habitat types and land-use systems. This method allowed more individuals to be studied than is logistically possible with traditional telemetry studies, providing sufficient sample sizes for between-species and between-sex comparisons. Activity was compared between broad habitats and with respect to the proximity of various natural features and anthropogenic factors. We also assessed the relative tolerance of jaguars and pumas to human activity, by comparing their responses with ecotourism within an otherwise undisturbed protected forest.

### METHODS

**STUDY SITE AND CAMERA TRAPPING.**—The study area covered ca 525 km<sup>2</sup>, spanning the eastern half of the Cockscomb Basin

Received 6 October 2009; revision accepted 9 February 2010.

<sup>3</sup>Corresponding author; e-mail: beccifoster@hotmail.com

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Wildlife Sanctuary (CBWS), comprising lowland subtropical secondary broadleaf forest, and the mosaic of unprotected habitats and land-use systems which extend from its eastern border toward the sea. The protected forest is partially buffered from human development by a band of unprotected forest, together forming a contiguous forest block. The unprotected fragmented landscape to the east of this forest block is a patchwork of pine savannah, shrubland and broadleaf forest, inter-dispersed with villages, milpa farms (slash and burn multi-crop fields), fruit plantations, cattle pastures and a single highway running north–south (Fig. S1). The diets of jaguars and pumas differ markedly in the study area (Foster *et al.* 2010). Both rely heavily on a single species of medium-sized prey: armadillos (*Dasypus novemcinctus*) for jaguars and pacas (*Agouti pacas*) for pumas, and supplement their diet with large ungulates: mainly peccaries (*Tayassu pecari* and *Pecari tajacu*) and livestock for jaguars, and deer (*Mazama americana*) and peccaries for pumas. Illegal hunting of game species occurs at the periphery of CBWS. It is nevertheless likely that wild prey abundances are lower outside the protected forest where the habitat is fragmented by pastures and monocultures, and unregulated hunting is common (Harmsen 2006, Foster 2008). Jaguar density across the study area has been estimated from camera-trap data at  $\sim 7$  individuals/100 km<sup>2</sup>, ranging from *ca* 10/100km<sup>2</sup> in CBWS to 2/100 km<sup>2</sup> in fragmented lands (Harmsen 2006, Foster 2008). Puma density is unknown, with too many unidentifiable photo captures in CBWS to reliably identify all individuals (Harmsen 2006), and too few elsewhere for reliable abundance estimates (*cf.* Kelly *et al.* 2008); however, short-term small-scale recognition of pumas from CBWS camera-trap photos indicates fewer pumas than jaguars (Harmsen *et al.* 2010).

Camera-trap data were collected across the study area from 178 locations, totaling *ca* 22,000 trap-nights over 3 yr (2004–2006). The distance between neighboring stations averaged 0.8 km (*SD* = 0.8 km, *N* = 178). The furthest distance between any two stations was 39 km. Outside CBWS, where high levels of nontarget daytime traffic were unavoidable (*e.g.*, vehicles, cattle and people) cameras were operational only at night. Because jaguars and pumas in the study area are primarily nocturnal with high overlap in activity pattern (Harmsen *et al.* 2009), it was deemed appropriate to use only night captures in the analyses.

**HABITAT USE BY JAGUARS AND PUMAS.**—Photographed jaguars were sexed and individually identified based on pelage patterns. Pumas were not sexed or individually identified because long-term large-scale individual recognition of pumas inhabiting the study area was unreliable (Harmsen 2006). Habitat use by jaguars and pumas was calculated at each camera station as (1) presence–absence and (2) activity: the absolute capture rate per 28 nights (total number of captures/trap effort  $\times$  28). The mean time that a camera was operational until its first jaguar capture was 22.8 d (*SE* =  $\pm 2.1$ , *N* = 81) inside the protected forest and 16.2 d (*SE* =  $\pm 2.7$ , *N* = 57) outside. Analyses of presence/absence therefore excluded stations with  $< 28$  d of uninterrupted trap effort if there were no cat captures. Analyses of capture rate excluded all stations with  $< 28$  d of uninterrupted trap effort. Thus, activity was only calculated for locations

with cameras that functioned for  $\geq 1$  mo, allowing comparison between species at any location.

**HABITAT CLASSIFICATION OF CAMERA LOCATIONS.**—Camera stations were categorized as within or outside the single forest block (Fig. S1, protected forest plus unprotected buffer). Some areas of the forest block adjoined forest-milpa: areas of forest dominated by milpa and cacao farms. Although a continuation of forest cover, forest-milpa was interspersed with small-scale farms and frequently used human trails.

Stations were classified as protected forest, unprotected forest buffer, disturbed forest (all forest patches, dense shrublands, milpa and forest-milpa), savannah (including transitional zones to forest) or pasture. For every station, distances were calculated to settlements, major roads, flowing water, pastures, plantations, forest block, disturbed forest and savannah.

Streams or trails may function as funnels, facilitating movement of cats through dense vegetation. Funnels included permanent or seasonal man-made trails, streams, unpaved roads and buffers around the edge of pastures where natural vegetation had been cleared. Funnel width (hereon ‘trail width’) at each station was calculated as the mean of three measurements: 0 m and  $\pm 20$  m from the station, following Harmsen *et al.* (2010).

**ASSUMPTIONS AND VALIDATIONS.**—In the absence of any other available measure, absolute capture rate is used to index activity levels in different habitats. This requires assuming that the variation in detectability between camera traps is constant within and between species, sexes and habitats, which cannot be tested directly. Two independent measures of big cat presence were used to help validate this assumption indirectly at least for some of the species-sex-habitat combinations: (1) scats were collected opportunistically and genotyped as either jaguar or puma (Foster *et al.* 2010) and (2) the numbers and sexes of pumas and jaguars killed by people outside the protected forest were monitored over 31 mo through discussions with locals (detailed in Foster 2008). Similarity between scat and camera data would indicate that the camera methodology was not biased in detecting presence/absence of jaguars and pumas, and similarity between mortality and camera data would indicate that the camera methodology was not biased in detecting pumas, or jaguars of either sex, in the human-matrix. Because male jaguars in the study area are known to range further than females (Harmsen 2006, Foster 2008), we expected *a priori* an overall higher detectability of male than female jaguars.

**STATISTICAL ANALYSES.**—Frequencies of locations with and without big cats were calculated across categories of habitat, species and sex (jaguars only) and analyzed by chi-square, with *post-hoc* partitioning following Siegel and Castellan (1988). Jaguar and puma activities were compared at locations where both species were present. Because pumas were present at so few sites in the fragmented landscape, this analysis was limited to locations within the forest block.

A two-factor general linear model (GLM) with repeated measures on the random factor camera station (Doncaster & Davey 2007) tested for variation in jaguar activity with jaguar sex and

habitat type:  $Jaguar\ activity = sex|habitat + station'(habitat) + \epsilon$ . Stations with zero jaguar activity were excluded.

Inside the forest block, jaguar activity was investigated in relation to: trail width, distance to water, distance to human settlement and activity of jaguars of opposite sex. Outside the forest block, additional distance variables were investigated: distances to the forest block, disturbed forest, savannah, pasture, plantation and major roads. Spearman rank correlations were used to assess the strength and direction of the relationship between each variable, and, where appropriate, stepwise regression was used to select the most parsimonious model of variation in jaguar activity. Variation in puma activity within the forest block in relation to trail width, distance to water, distance to human settlement and jaguar activity was investigated following the same method. Data were square root or  $\log_{10}$  transformed to normalize the residuals for GLM and regression analyses where necessary.

**TOLERANCE OF JAGUARS AND PUMAS TO HUMAN DISTURBANCE.**—The hypothesis that cat activity declines with increased human disturbance was tested by analyzing the response of big cat activity on the CBWS access road to tourist visitation rates in the reserve, as a proxy for disturbance. The 10 km unpaved road, the only access for tourists, runs from the highway through unprotected forest and terminates 2.5 km into CBWS (Fig. S1). Visitor activity per 28 d was calculated from CBWS records for each calendar month as {visitors per mo/mo length (in d)  $\times$  28}. A camera was maintained on the road at the reserve boundary from January 2004 until May 2007 and jaguar and puma activity per 28 d was calculated each calendar month. Data were excluded for months when no visitor statistics were available or trap effort was < 28 nights. The activities of jaguars and pumas were compared, as were the number of months during which each species used the road. The activity of each species was regressed against visitor activity.

## RESULTS

**HABITAT USE BY JAGUARS AND PUMAS.**—Over the 3-yr period, we obtained 1380 photo captures of jaguars and pumas. We identified 64–74 individual jaguars. Individual identification of pumas was not possible (Harmsen 2006). Within the forest block, the relative frequencies of stations with and without big cat visits did not differ between jaguars and pumas ( $\chi^2_1 = 0.179$ ,  $P > 0.1$ , of 104 locations 60 had jaguars and 63 had pumas). Outside the forest block, in contrast, more locations reported jaguars than pumas (47/67 locations were visited by big cats, all by jaguars and only seven by pumas,  $\chi^2_1 = 49.6$ ,  $P < 0.0001$ ). Fewer puma than jaguar scats were found outside than inside the forest block (3:66 outside:inside for puma compared with 51:224 for jaguar,  $\chi^2_1 = 8.4$ ,  $P = 0.004$ ) suggesting that the jaguar bias outside the forest block observed using cameras is not an artifact of the methodology (*i.e.*, night-only trapping, or spacing of cameras relative to home range size). Moreover, 11 jaguars and no pumas were known to have been killed outside the forest block during the study period, primarily on farms (Foster 2008).

Despite the relative scarcity of pumas in the fragmented landscape, at locations in the forest block where both jaguars and pumas

were captured, they showed no significant differences in site usage (mean difference in visits per 28 d  $\pm$  95% =  $0.379 \pm 0.472$ ,  $N = 44$ , paired-sample  $t = 1.62$ ,  $P > 0.10$ ). The mean jaguar activity  $\pm$  SE was  $1.7 \pm 0.2$  captures per 28 nights and mean puma activity was  $1.3 \pm 0.2$ .

Both inside and outside the forest block, male jaguars were present at more locations than females (males visited 57 of 102 forest block locations, females visited 18,  $\chi^2_1 = 33.1$ ,  $P < 0.0001$ ; males visited 37 of 63 locations outside forest block, females visited 18,  $\chi^2_1 = 11.6$ ,  $P < 0.0001$ ).

The presence–absence of male jaguars showed no broad-scale habitat associations ( $\chi^2_4 = 8.8$ ,  $P > 0.05$ ; Table 1) but they were nevertheless present at a high proportion of the pasture locations (17/21), relative to their presence at all other locations (75/143, partitioned  $\chi^2_1 = 6.3$ ,  $P < 0.05$ ). Female jaguars were present at a high proportion of disturbed forest locations and absent from many of the protected forest sites ( $\chi^2_4 = 19.0$ ,  $P < 0.002$ ; Table 1). Females were recorded at few protected forest locations (9/81) relative to their presence at all other locations (25/71, partitioned  $\chi^2_1 = 13.0$ ,  $P < 0.001$ ). Note that variation in trap effort between the habitats had no perceptible influence on the detection of jaguars. For each habitat, trap effort at locations that did not detect jaguars was greater than trap effort until first capture at locations that did detect jaguars (Kruskal–Wallis test: males  $N = 161$ ,  $H = 65.9$ ,  $df = 9$ ,  $P < 0.0001$ ; females  $N = 153$ ,  $H = 21.5$ ,  $df = 9$ ,  $P < 0.02$ ).

Across the study area, male jaguars were no more likely to be present at locations within 50 m of forest (present at 81/149 sites) than those > 50 m from forest (present at 13/17 sites,  $\chi^2_1 = 3.0$ ,  $P > 0.05$ ). This was also true for females (present at 34/143 sites < 50 m from forest and at 2/10 sites > 50 m from forest,  $\chi^2_1 = 0.3$ ,  $P > 0.5$ ), though males were detected up to 438 m from forest (at the camera location second farthest from forest within the camera network), whilst females were not detected at locations over 178 m from forest.

Jaguar activity showed sex-dependent habitat use (Sex  $\times$  Habitat interaction in Table 2). Male activity tended to be higher than female activity, with the difference between males and females declining from 50-fold greater in the protected forest, through forest buffer, savannah, pastures, to negligible difference in the disturbed forest (Fig. 1). The number of individual males and females detected in these habitats showed a similar pattern (Foster 2008).

TABLE 1. Number of locations with and without jaguars across five habitats.

	Protected	Buffer	Savannah	Pasture	Disturbed	Total
<b>Males</b>						
Presence	42	10	8	17	12	89
Absence	39	6	5	4	17	71
Total	81	16	13	21	29	160
<b>Females</b>						
Presence	9	7	1	5	12	34
Absence	72	9	10	10	16	117
Total	81	16	11	15	28	151

TABLE 2. General linear model of jaguar activity with sex and habitat, using Type-II adjusted MS.

Source	df	Seq. MS	Adj. MS	F	P-value
Sex	1	19.9	19.0	106	< 0.0001
Habitat	4	0.31	0.31	1.39	> 0.2
Sex × Habitat	4	1.59	1.59	8.85	< 0.0001
Station'(Habitat)	82	0.22	0.22	1.23	> 0.1
Error <sup>a</sup>	82	0.18	0.18		
Total	173				

<sup>a</sup>Error variation for interaction is the highest order term in the model: sex × station'(habitat).

A similar number of males (seven) to females (five) were killed outside the protected forest during this period (Foster 2008). All deaths, except for that of one male, occurred outside the forest block. These mortality counts imply that male and female jaguars frequent the human-matrix with similar intensity. Therefore, we can assume that the negligible difference observed between male and female capture rates in the pastures and disturbed forest (Fig. 1) reflects real similarities in activity rather than differential detectability of the two sexes in these habitats.

Across the forest block, male jaguar activity correlated positively with trail width ( $\rho_s = 0.496$ ,  $P < 0.001$ ,  $N = 51$ ), and with female activity ( $\rho_s = 0.289$ ,  $P < 0.05$ ,  $N = 54$ ), but not with distance from water or settlements (both  $P > 0.1$ ,  $N = 54$ ). Trail width also correlated negatively with distance from settlements: trails were narrower further in to the core of forest block ( $\rho_s = -0.450$ ,  $P < 0.001$ ,  $N = 51$ ). Stepwise regression suggested that trail width

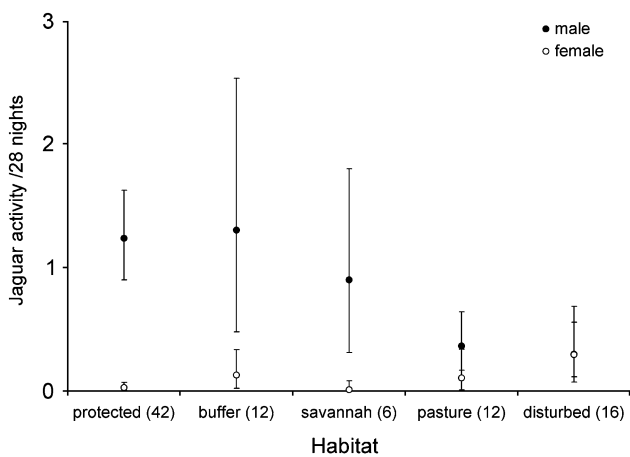


FIGURE 1. Jaguar activity in five habitats based on night captures from camera-trap data. Locations with zero jaguar activity (neither sex present) are excluded; all cameras functioned  $\geq 28$  continuous nights. Sample sizes indicate number of stations in each habitat. Means and 95% CI shown are back-transformed from square-root values. 'Protected' refers to protected forest; 'buffer' refers to unprotected forest contiguous with protected forest; 'disturbed' refers to milpa-forest, milpa, shrublands and forest fragments.

best explained variation in male activity (square root male activity =  $0.363 + 0.0558$  square root trail width:  $F_{1,49} = 23.4$ ,  $P < 0.0001$ , adjusted  $R^2 = 31\%$ ) as previously demonstrated in CBWS (Harmsen *et al.* 2010).

Within the forest block, female jaguar activity correlated negatively with distance from water ( $\rho_s = -0.548$ ,  $P < 0.05$ ,  $N = 17$ ), but not with trail width, distance from settlements or male activity (all  $P > 0.1$ ,  $N = 17$ ). Distance from water best explained variation in female activity ( $F_{1,15} = 6.20$ ,  $P < 0.05$ , adjusted  $R^2 = 25\%$ ; Fig. 2).

Outside the forest block, activity of male jaguars positively correlated with distance from pasture ( $\rho_s = 0.396$ ,  $P < 0.05$ ,  $N = 28$ ) and from plantations ( $\rho_s = 0.423$ ,  $P < 0.05$ ,  $N = 28$ ). Both variables were positively correlated with each other ( $\rho_s = 0.489$ ,  $P < 0.01$ ,  $N = 28$ ) and with distance from settlements (pasture  $\rho_s = 0.632$ ,  $P < 0.01$ ,  $N = 28$ ; plantation  $\rho_s = 0.466$ ,  $P < 0.05$ ,  $N = 28$ ). Although these variables are confounded, the data suggest that male activity declined with proximity to areas of human development in general. In contrast to the forest block, male activity did not vary with trail width ( $P > 0.5$ ,  $N = 26$ ).

Outside the forest block, female activity correlated only with distance from contiguous forest ( $\rho_s = 0.584$ ,  $P < 0.02$ ,  $N = 18$ ) and not with trail width, male activity, distances to water, major roads, settlements, disturbed forest, pastures, plantations or savannahs (all  $P > 0.1$ ,  $N = 18$ ). Distance from the forest block best explained variation in female activity ( $F_{1,16} = 12.3$ ,  $P < 0.01$ , adjusted  $R^2 = 40\%$ ); however, two outliers had unusually high leverage because they were both far from the forest block (*ca* 500 m apart on the same road). Analyses re-run without this pair indicated a positive correlation of female activity with proximity to major roads ( $\rho_s = 0.647$ ,  $P < 0.01$ ,  $N = 16$ ) and that variation in female activity was now best explained by proximity to major roads and distance from the forest block (constant  $t = 5.70$ , major road  $t = -3.60$ , forest block  $t = 2.43$ ,  $P < 0.05$  for all, adjusted  $R^2 = 50\%$ ). This

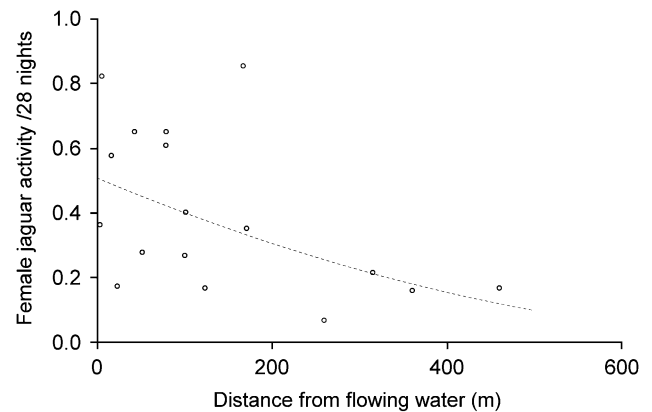


FIGURE 2. Variation in female jaguar activity with distance from water within forest block, based on data from 17 camera stations. Locations with zero activity are excluded; all cameras functioned  $\geq 28$  continuous nights. Square-rooted female activity =  $0.713 - 0.000797 \times \{\text{square-rooted distance from water}\}$ :  $F_{1,15} = 6.20$ ,  $P < 0.05$ , adjusted  $R^2 = 25\%$ . Curved line shows back-transformed regression.

implies that female jaguar activity was higher closer to areas of human development, further from the forest block and nearer the major roads. Although this contrasts with the pattern observed for male jaguars outside the forest block, there was little difference between the sexes in pastures or disturbed forest habitats, both associated with human development. Thus, although male activity declines closer to human development and female activity increases, the net result is that both sexes have similar rates of activity at these locations (Fig. 1).

Inside the forest block, puma activity positively correlated with jaguar activity ( $\rho_s = 0.316$ ,  $P < 0.02$ ,  $N = 58$ ) suggesting that the two species use forest block locations with similar habitat attributes; indeed puma activity positively correlated with trail width ( $\rho_s = 0.326$ ,  $P < 0.02$ ,  $N = 55$ ), but not with distance to settlements or water ( $P > 0.2$ ,  $N = 59$ ). As before, trail width correlated negatively with distance from settlements ( $\rho_s = 0.451$ ,  $P < 0.001$ ,  $N = 55$ ). Stepwise regression selected trail width as the single best predictor of puma activity, although little variation was explained by this variable ( $F_{1,53} = 5.06$ ,  $P < 0.05$ , adjusted  $R^2 = 7\%$ ). Given that male and female jaguars respond differently to habitat variables, variation in puma activity may be better explained if the data could be separated between the sexes.

**TOLERANCE OF JAGUARS AND PUMAS TO HUMAN DISTURBANCE.**—Visitor rates to CBWS ranged from 88 to 787 people per month. Jaguars were present on the road during more months than pumas (jaguars 30/31 mo, pumas 16/31 mo,  $\chi^2_1 = 16.5$ ,  $P < 0.0001$ ) and were more active (jaguar mean  $\pm SE = 4.74 \pm 0.54$  per 28 nights, puma  $2.00 \pm 0.34$  per 28 nights,  $t_{43} = 4.27$ ,  $P < 0.0001$ ).

Jaguar use of the road decreased during peak tourist periods when vehicle intensity along the road and human activity were both high. Overall, jaguar activity declined linearly with increasing visitor activity (regression:  $F_{1,29} = 5.84$ ,  $P < 0.05$ , adjusted  $R^2 = 14\%$ ; Fig. 3). Puma activity was not associated with visitor rate ( $\rho_s = 0.100$ ,  $P > 0.5$ ,  $N = 31$ ). Although there was no detectable decline in puma activity with human activity, the high frequency of months during which pumas avoided the road, and their relatively low activity when present compared with jaguars, suggests that pumas may be less tolerant of human disturbance than jaguars.

## DISCUSSION

The few published studies of sympatric jaguar and puma populations show similar daily activity patterns in homogenous forests (Núñez *et al.* 2002, Harmsen *et al.* 2009). In the dry forests of Mexico, jaguar and puma ranges overlapped spatially and both species were associated with streams, which provided easy travel routes through the dense vegetation (Núñez *et al.* 2002). Emmons (1987) detected subtle differences in habitat use in Peruvian lowland rain forest, where only jaguars associated with rivers, reflecting prey selection rather than accessibility. Harmsen *et al.* (2009) demonstrated complete spatial overlap of jaguars and pumas in the homogenous protected forest of CBWS, combined with temporal segregation.

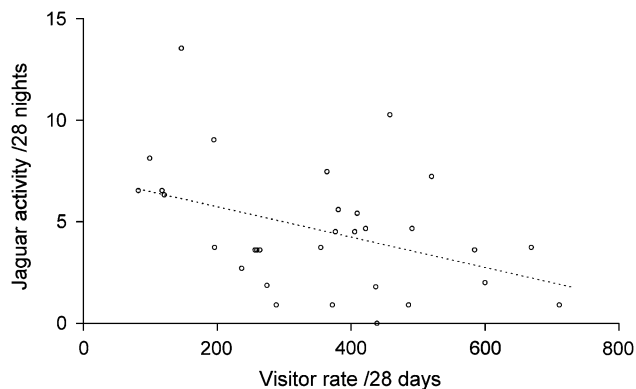


FIGURE 3. Variation in monthly jaguar activity with visitor rates in protected forest, based on data from 31 mo, January 2004 to May 2007. All cameras functioned  $\geq 28$  continuous nights per month. Jaguar activity =  $7.24 - 0.00749 \{ \text{visitor rate} \}$ ;  $F_{1,29} = 5.84$ ,  $P < 0.05$ , adjusted  $R^2 = 14\%$ .

Throughout the forest block of this study, jaguars and pumas were present at a similar number of locations and used the sites with similar intensity, emphasizing the extraordinary capacity for coexistence of these morphologically similar predators. Activity of pumas and male jaguars increased with path width (*cf.* Harmsen *et al.* 2010 in protected forest). Wide trails and unpaved roads within dense forest vegetation may facilitate movement (Rabinowitz & Nottingham 1986, Dickson *et al.* 2005), and potentially hunting and olfactory communication (Harmsen 2006). Given the similarities in jaguar and puma habitat use throughout the forest, their coexistence may depend on dietary segregation (Foster *et al.* 2010).

Heterogeneous landscapes provide opportunities for inter-specific habitat partitioning. Where jaguars and pumas are sympatric in mosaic landscapes, pumas reportedly use more open habitats than jaguars, including disturbed areas such as croplands and pasture (Scognamillo *et al.* 2003, Silveira 2004). Conversely, jaguars reportedly favor forest over exposed areas such as pasture (Schaller & Crawshaw 1980, Crawshaw & Quigley 1991, Silveira 2004, Cullen *et al.* 2005). In this study, however, jaguars were common and pumas scarce outside the forest block. This was unexpected, given the greater range of habitats associated with pumas than jaguars (Sunquist & Sunquist 2002). Here, we present four potential explanations:

(1) *Pumas are heavily hunted by humans:* Persecution is unlikely to account for the rarity of pumas outside the forest block. In contrast to jaguars, no puma deaths were verifiably human-induced during the study period, the most recent report dated to *ca* 2000 (Foster 2008). We have no reason to suspect that hunting of pumas was under reported compared with jaguars. Unlike jaguars, pumas were rarely detected on cattle farms (jaguars were photographed every 10–100 trap-nights on seven of eight cattle farms, whereas pumas were only photographed on one of the cattle farms, with one capture every 1000 trap-nights). There was no evidence that pumas preyed on livestock (Foster *et al.* 2010) and they were seldom held responsible for losses, whereas blame was attributed to jaguars, crocodiles, snakes and people (Foster 2008). The international fur

trade has historically focused on spotted cats (Smith 1976, McMahān 1982, Nowell & Jackson 1996, Payán & Trujillo 2006) so it is unlikely that illegal markets target the plain-coated puma over the jaguar.

(2) *Pumas have a low tolerance of human disturbance*: Studies of pumas demonstrate temporal and/or spatial avoidance of human activity (van Dyke *et al.* 1986, Janis & Clark 2002, Dickson *et al.* 2005, Sweanor *et al.* 2008). It remains unclear, however, whether these are direct effects or the result of prey avoiding human activity (*e.g.*, Sweanor *et al.* 2008). No published data exist on the response of jaguars to human disturbance. We found that jaguar activity declined during months of increased tourist activity. Although pumas showed no detectable response to tourist activity, they completely avoided the disturbed site during half the study period; while at other sites throughout the protected forest they had similar activity as jaguars. This suggests a lower tolerance of pumas than jaguars to human disturbance. Pumas tend to be smaller than jaguars in regions of coexistence (Iriarte *et al.* 1990), and intra-guild competition may result in the puma adopting more cautious behaviors. Jaguars and pumas show spatio-temporal segregation in CBWS, though it is unknown whether this is mutual or imposed by one species (Harmsen *et al.* 2009).

(3) *An essential resource, present in forest block, is lacking outside it*: As pumas persist in a wide range of vegetative and environmental conditions (Sunquist & Sunquist 2002), it seems unlikely that specific microhabitat requirements impeded their survival outside the forest block in this study. Scognamillo *et al.* (2003) suggested that the availability of appropriate medium-sized prey may facilitate jaguar and puma coexistence. The low availability or absence of a key prey species may shift the balance in favor of one or the other. Pacas, deer and peccaries are all popular game species in Belize, and important prey of pumas (Foster *et al.* 2010). It is possible that puma use of the human-matrix is restricted by prey availability, which may be limited by exploitative competition with game hunters (Foster *et al.* 2010). Such propositions need proper qualification by studying wild prey abundance and harvest by hunters.

(4) *Pumas are excluded by jaguars outside the forest block*: Within carnivore guilds, subordinate species may be displaced to marginal habitats (Woodroffe 2001). Thus, where jaguars and pumas coexist, we may expect displacement of pumas from the forest to less optimal areas. We found no evidence, however, that pumas were displaced to the human-matrix by jaguars, rather pumas were rarely detected in the fragmented lands and were more common where jaguar density was highest in the forest block. Pumas may conceivably be excluded from the human-matrix by jaguars, though there is no evidence for this across their range; rather, pumas reportedly occupy disturbed or fragmented habitats both with and without jaguars (Leite & Galvão 2002, Michalski & Peres 2005, Lyra-Jorge *et al.* 2008, Walker & Novaro 2009). A formal test of competitive exclusion would require experimental removal of jaguars, which is both unethical and impractical. It seems unlikely that pumas are excluded by exploitative competition with jaguars in this area, given their low dietary overlap (Foster *et al.* 2010).

Although jaguars were detected in all habitat types, and around all land-use systems, their habitat use differed between the

sexes. Males were present at more locations than females across the study area. This is expected because males have larger home ranges than females and consequently a higher probability of encountering a camera (Foster 2008). Males dominated the protected forest, both in terms of the number of individuals using a given location (Foster 2008, Harmsen *et al.* 2009), and the intensity of use (this study). In the forest block, male activity increased on wider trails; for females, higher activity was associated with proximity to flowing water. This disparity may reflect differences in hunting preferences, or may be a strategy for females with young to avoid infanticide by males attempting to gain mating opportunities. Whilst males dominated the wider trails to traverse the forest, females may have favored watercourses as safer travel routes through the dense habitat. CBWS's high density of waterways (*ca* 2.5 km/km<sup>2</sup>) may provide alternative routes through the forest, potentially explaining the low detection of females on trail-based cameras in this habitat (*e.g.*, Harmsen 2006).

Male carnivores tend to be more risk-prone than females, making them more susceptible to conflict with humans (Linnell *et al.* 1999). Our study found no evidence that females were less tolerant of lands with human activity than were males. In fact, outside the forest block both sexes appeared similarly active when present in disturbed areas, and were equally susceptible to human-induced mortality. This is concerning, as the removal of adult females has a greater impact on the population than the removal of males (Foster 2008).

CONSERVATION IMPLICATIONS.—Although pumas remain widespread across the Americas, their populations are in decline and their status is poorly known in Central America (Reid 1997, Caso *et al.* 2008, Laundré & Hernández 2009). In North America, where pumas exist without jaguars, the greatest threat to their long-term survival is habitat loss, primarily associated with extensive urbanization (Logan & Sweanor 2001). In the neotropics, where pumas coexist with jaguars, it is often proposed that they may frequent more open habitats and are better adapted at using human-altered landscapes (*e.g.*, Núñez *et al.* 2000, Caso *et al.* 2008). Our findings contradict this; rather, the observed restriction of pumas to the forest block implies that further deforestation could lower puma carrying capacity in the area. Although pumas are well known to inhabit desert and arid scrub with minimal vegetation (Logan & Sweanor 2001, Walker & Novaro 2009) other studies have shown that they favor dense understory (Beier 2009). It is difficult to separate the influence of habitat *per se*, from prey availability, competition with other predators (jaguars or people) and human disturbance. Foster *et al.* (2010) suggested that regulating game hunting, particularly pacas and ungulates, may assist puma survival in the fragmented lands outside the forest block. Even if suitable prey is abundant, however, sensitivity to human activity may prevent pumas from using the increasingly human-influenced landscape.

Jaguars were detected up to 438 m from forest cover (< 200 m for females), and used the different habitats present in this area of Belize. Although we cannot extrapolate nationally, it seems that the current level of development and deforestation does not

yet prevent jaguar movement through this area in southeast Belize. However, a functional corridor for any big cat species will not only require suitable habitat with adequate connectivity, but also sufficiently low levels of lethal persecution and game hunting. The apparent willingness of jaguars to frequent the human-influenced landscape in Belize presents a conservation paradox. It has positive implications for the successful establishment of a functional corridor connecting jaguar conservation units across their geographic range (Rabinowitz 2006), but simultaneously puts them at increased risk of contact with humans, livestock and persecution.

## ACKNOWLEDGMENTS

This study was funded by the Wildlife Conservation Society, the UK Natural Environment Research Council, Panthera, the Liz Claiborne Art Ortenberg Foundation, the North of England Zoological Society, Brevard Zoo and Woodland Park Zoo. The Belize Audubon Society was a partner in the research and provided logistical support as well as data on CBWS visitor rates. We thank all of its park wardens in CBWS for their cooperation. We also thank E. Pop for field assistance and invaluable field expertise, F. Yau for his fieldwork contribution and the numerous landowners who gave permission to work on their properties. We thank S. Silver and L. Ostro for initiating and facilitating our research in CBWS, and A. Rabinowitz for his continued support.

## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

FIGURE S1. Study area habitats, land use and major rivers, showing camera stations.

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